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1 **Beyond forest habitat qualities: climate and tree characteristics as the major drivers of epiphytic**
2 **macrolichen assemblages in temperate mountains**

3

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19

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22 Bauges Natural Regional Park).

23 **ABSTRACT**

24 Question

25 How are epiphytic macrolichen assemblages shaped by forest habitat quality as reflected by the
26 availability of late-developmental forest attributes (i.e. stand maturity) and the temporal continuity
27 of the wooded state (i.e. forest continuity)? Are these two forest habitat features the main drivers of
28 lichen assemblages, and if so, at which spatial scale?

29 Location

30 Temperate mountain forests in the French Northern Alps.

31 Methods

32 In our sampling design, we defined treatments by crossing forest continuity (ancient vs recent) and
33 stand maturity (mature vs overmature), then quantified lichen response to the treatments at the
34 stand (n = 70) and tree scales (n = 420). We distinguished between total macrolichen and *Lobarion*
35 species alone. Finally, we assessed the influence of tree-, stand- and landscape-scale variables, as
36 well as climatic variables.

37 Results

38 Neither total macrolichen nor *Lobarion* diversity and composition were influenced by forest
39 continuity, stand maturity or by stand- or landscape-associated variables. Instead, climatic variables,
40 light availability at the stand scale and host tree characteristics were the major drivers of lichen
41 assemblages. In our mountain forests, this clearly shows that macrolichen were more influenced by
42 local abiotic and biotic factors than by present or past human-induced activities.

43 Conclusions

44 Overall, we show that assemblage patterns in forest ecosystems may be driven by parameters which
45 are not directly related to habitat quality. The influences of forest continuity and stand maturity on
46 diversity and composition thus appear to be context-dependent. In the ecological context of alpine
47 forests, these findings highlight the benefits of selective-cutting practices and illustrate the
48 importance of structural heterogeneity, in terms of both improved accessibility to light and tree

49 diameter diversity. Finally, the importance of temperature in shaping assemblage patterns suggests
50 that global warming is probably the most significant threat to macrolichen conservation in temperate
51 mountain forests.

52

53 Keywords: ancient forest, biodiversity conservation, epiphytic macrolichens, forest management,
54 habitat quality, mountain forest, diversity patterns

55

56 **INTRODUCTION**

57 Biodiversity patterns are shaped by numerous environmental factors acting at multiple spatial scales
58 (Levin 1992; Rosenzweig 1995). In forest ecosystems, species repartition may be influenced by
59 climatic conditions at the large scale (Stevens 1989), by habitat amount and connectivity at the
60 landscape scale (Fahrig 2013), by forest structure and composition at the stand scale (Barbier et al.
61 2008) and by deadwood or tree-related microhabitats at the tree scale (Müller et al. 2014). Overall it
62 is now fairly well accepted that forest biodiversity is mostly influenced by two inherent and non-
63 exclusive habitat qualities: stand maturity and forest continuity.

64 Stand maturity refers to a continuous process of tree and stand ageing, which depends on tree
65 lifespan, the traditional harvest age of the dominant tree species and type of forest management.

66 When comparing managed and unmanaged forests (e.g. Nascimbene et al. 2007; Nascimbene, Thor,
67 et al. 2013) or young and old forests (e.g. Fenton & Bergeron 2008; Fritz, Niklasson, et al. 2008),
68 numerous studies have pointed out the importance of stand maturity for forest biodiversity.

69 Specifically, the availability of deadwood attributes or of very large trees has been shown to enhance
70 the conservation of specialized species, such as some insects (e.g. Nilsson & Baranowski 1997),
71 bryophytes (e.g. Spitale & Mair 2015) or birds (e.g. Bütler et al. 2004). This awareness has led to the
72 development of silvicultural systems better able to increase, or at least maintain, stand maturity
73 attributes and support multifunctional forests (Gustafsson et al. 2012).

74 Forest continuity refers to the maintenance of forest cover over time, regardless of stand maturity
75 and management type. In Europe, forest continuity is closely related to the reforestation of previous
76 agricultural areas since the mid-nineteenth century. We distinguish between ancient forests, which
77 have existed continuously for centuries, and recent forests, which result from reforestation after a
78 certain threshold date (Hermy & Verheyen 2007). Forest continuity has been shown to play a
79 fundamental role in temperate forests for herbaceous plant assemblages (Hermy & Verheyen 2007),
80 ectomycorrhizal fungi (Diedhiou et al. 2009), lichens and mosses (Fritz, Gustafsson, et al. 2008) and
81 insects (Gossner et al. 2008). Two limitation processes have been highlighted: the poor dispersal
82 ability of many ancient-forest species, impeding their colonization of recent forests (e.g. Verheyen et
83 al. 2003); and recruitment limitations due to soil changes and competitive interactions (e.g. Honnay
84 et al. 2002). Conservation strategies in several European countries now recommend primarily
85 focusing on ancient forests (e.g. Fritz, Gustafsson, et al. 2008; Pătru-Stupariu et al. 2013).

86 Epiphytic lichens are among the most sensitive species groups known to respond to both stand
87 maturity and forest continuity (Ellis 2012). Previous work has shown that epiphytic lichen diversity
88 increases with stand maturity (Ranius et al. 2008; Moning et al. 2009; Nascimbene et al. 2009).
89 Consequently, overmature stands are expected to host a larger epiphytic lichen diversity than
90 mature stands (Nascimbene, Thor, et al. 2013). Also, few studies have pointed out the link between
91 forest ancientness and epiphytic lichen assemblages (Rose 1976; Fritz, Gustafsson, et al. 2008;
92 Marmor et al. 2011). Some lichen species have even been proposed as ancient forest indicators in
93 England (Rose 1976) or in Sweden (Nitare & Norén 1992). Many of these indicator species have strict
94 ecological requirements, such as the cyanolichens (Kuusinen 1996; Hedenås & Ericson 2008) or the
95 *Lobarion pulmonariae* community (James et al. 1977; Ellis & Coppins 2007), and most of them are of
96 conservation concern.

97 Although several studies have demonstrated the importance of overmature stands for lichen
98 conservation, to the best of our knowledge, no studies have controlled for the potential cumulative
99 effect of forest continuity. Moreover, in a recent review, Nascimbene et al. (2013) pointed out that

100 the effect of forest continuity on lichen assemblage patterns has still rarely been explored despite
101 the fact that this information is crucial to improving conservation-oriented management. Among
102 epiphytic lichens, macrolichens (i.e. species with large thallus, restricted to fruticose, foliose and
103 squamulose species in this study) and crustose lichens have both been shown to respond similarly to
104 habitat alterations. Macrolichens, much easier to sample and to identify, could be good indicators of
105 the conditions required by the entire lichen community (Bergamini et al. 2005). They are therefore
106 often used as a proxy to assess the effect of forest management on total lichen diversity (e.g. Uliczka
107 & Angelstam 1999; Nascimbene et al. 2009). At the same time, the *Lobarion* species belong to a
108 community of epiphytic macrolichen sensitive to climate (i.e. cold-humid climate niche) and habitat
109 quality (i.e. forest continuity) and are expected to be good indicators of old-growth forests (Kuusinen
110 1996; Hedenås & Ericson 2008).

111 Here, we tested whether the diversity and composition of total and *Lobarion* epiphytic macrolichen
112 responded to forest continuity and stand maturity. As shifts in assemblage patterns are likely to
113 result from a complex of different factors acting at different spatial scales (Jüriado et al. 2009; Király
114 et al. 2013; Ódor et al. 2013), we also tested the relative influence of a set of tree-, stand- and
115 landscape variables on epiphytic macrolichens, as well as climatic variables. Landscape variables
116 were used to consider possible drivers underlying the effect of forest continuity, e.g. related to
117 differences in the amount of favorable habitat in the surrounding landscapes at ancient and recent
118 forest sites. Stand and tree variables were used to account for important local characteristics that
119 may structure epiphytic macrolichen communities, beyond the influence of stand maturity and forest
120 continuity. Based on this scheme, we addressed the following two questions: (i) Does forest
121 continuity or stand maturity shape epiphytic macrolichen assemblages? (ii) Among tree, stand,
122 landscape and climate factors, which have the greatest influence on epiphytic macrolichen
123 assemblages?

124

125 **MATERIALS and METHODS**

126 **Study area and experimental design**

127 The study was carried out in the French pre-Alps in the Vercors, Chartreuse and Bauges ranges
128 (Figure 1). These areas are characterized by a limestone substratum and a temperate climate. The
129 landscapes are mostly covered by unfragmented forests and afforestation has mainly occurred above
130 and below a persistent forest belt. Moreover, due to physical constraints and the lack of logging
131 roads, the forests in our study have hitherto been less intensively managed than lowland forests
132 (Paillet et al. 2015). Therefore, compared to recent lowland forests, recent mountain forests in the
133 Northern Alps are mostly adjacent to ancient forests and have the potential to develop towards
134 stand structures similar to those found in ancient forests.

135 In 2014, we sampled 70 sites located in mountain beech-fir forests at an altitude of 800 – 1500 m.
136 The dominant tree species were European beech (*Fagus sylvatica*), Silver fir (*Abies alba*) and Norway
137 spruce (*Picea abies*). Our stratified sampling design crossed forest continuity (ancient = 37; recent =
138 33) and stand maturity (mature = 33; overmature = 37), resulting in 22 ancient-mature sites, 15
139 ancient-overmature sites, 15 recent-mature sites and 18 recent-overmature sites. To insure
140 independence among observations and avoid edge effects, all the sampling sites were established > 1
141 km away from any of the other sites, were located in ancient or recent forests > 5 ha in area, and
142 were > 50 m from the nearest stand edge.

143 **Forest continuity and stand maturity**

144 Forest continuity was characterized by crossing digitized and georeferenced 1:40,000-scale État-
145 Major maps of France, charted in the middle of the 19th century, with 1:10,000-scale current
146 vegetation maps in a Geographic Information System managed with QGIS (QGIS Development Team
147 2015). Forest cover overlapping in both maps was considered to indicate ancient forests, while
148 current forest cover overlapping with crops, pastures or meadows in the État-Major maps was
149 considered to indicate recent forests. Around each of our selected ancient and recent forest sites
150 (500 m radius), we controlled the État-Major maps using 1:5,000 or 1:2,500 cadastral plans drawn

151 between 1730 and 1838. Finally, we used aerial photographs taken in the 1950s to confirm the
152 continuity of the forest cover since the middle of the 19th century, at and around each site.
153 Stand maturity was characterized on a 20-m-radius plot and a 10-m-radius subplot in which all
154 standing trees and lying trunks were recorded (for further details, see Janssen et al. 2016). Mean
155 canopy openness was estimated with a spherical densiometer from four points in the cardinal
156 directions, 10 m away from the plot center. To distinguish between mature and overmature stands,
157 we used hierarchical cluster analysis (Ward method) based on the first three axes of a principal
158 component analysis (PCA) considering four environmental variables closely related to stand maturity:
159 volume of large coarse woody debris ($\varnothing > 30$ cm), number of large snags ($\varnothing > 30$ cm), number of very
160 large living trees ($\varnothing > 62.5$ cm), and tree microhabitat diversity (cumulative inertia of 88.30%).

161 **Environmental variables**

162 To model the response of epiphytic macrolichens to forest continuity and stand maturity, we used
163 environmental variables in addition to continuity and maturity. Based on a recent review
164 (Nascimbene et al., 2013), we selected nine a priori biologically important variables (Appendix S1 &
165 Table 1). Climate variables – i.e. mean annual air temperature, total annual precipitation and mean
166 relative air humidity – were derived from the SAFRAN climatic model (Durand et al. 1993) and
167 adjusted for the effect of altitude following Kunstler et al. (2011). Landscape variables – i.e. distance
168 to nearest forest edge, land-use diversity and forest proportion (within a 500-m radius) – were
169 measured around each sampling site. Stand variables – i.e. mean canopy openness, total basal area
170 and the number of very large trees – were extrapolated from the measurements taken within each
171 20-m-radius plot. Finally, the diameter and species (fir, spruce, beech or other deciduous trees) of
172 the sampled trees were also considered.

173 **Species inventory**

174 Epiphytic macrolichens were surveyed in September, 2014, on the six largest live standing trees
175 inside a 20-m-radius circular plot (mean (\pm SD) diameter of sampled trees for ancient-mature sites =
176 47.4 (\pm 13.4) cm, ancient-overmature sites = 60.6 (\pm 20.9) cm, recent-mature sites = 47.0 (\pm 12.9) cm

177 and recent-overmature sites = 54.8 (± 20.1) cm). Samples for identification were collected mostly
178 from European beech (n = 182) and silver fir (n = 160) at each plot, but when these two species were
179 unavailable, Norway spruce (n = 50), Sycamore maple (*Acer pseudoplatanus*, n = 25), Common ash
180 (*Fraxinus excelsior*, n = 2) or Mountain elm (*Ulmus glabra*, n = 1) were sampled. Based on this
181 scheme, the cover percentage of each macrolichen species on each tree was visually estimated, from
182 the base of the trunk up to a height of 2 m, using 5% cover classes. Moreover, because it has been
183 shown that some groups of epiphytic lichens are more sensitive to stand maturity and forest
184 continuity, we distinguished in subsequent analyses between total epiphytic macrolichen and
185 *Lobarion pulmonariae* species, defined from James et al. (1977).

186 **Statistical analysis**

187 Analyses were performed with R version 3.3.2 (R Core Team 2017). Based upon data exploration, any
188 independent variables with a skewness >1 were log or log+1 transformed to approximate normal
189 distribution. For proportional data, logit transformation was applied. We then used two-way ANOVAs
190 with type III sum of squares to test the significance of climate, landscape and stand variables to
191 forest continuity, stand maturity and their interaction (Table 1).

192 To determine whether total and *Lobarion* epiphytic macrolichens richness and cover at the plot scale
193 (n = 70) were influenced by forest continuity, stand maturity or their interaction, we used two-way
194 ANOVAs. We then investigated whether diversity patterns were predicted by climate, stand or
195 landscape variables, using 48 a priori candidate linear models, plus the null model (Appendix S2).
196 Because richness and cover may not be independent, we also assessed model performance with
197 standardized richness by including "Cover" as a covariate. Also, because significant differences in
198 total richness and cover between the three mountain ranges were identified, we added "latitude" as
199 a covariate in all the candidate models. We then fit Poisson linear models for richness and negative
200 binomial linear models for cover and controlled for multicollinearity among explanatory variables
201 with variance inflation factors. The variance explained by the GLMs was estimated with the adjusted
202 coefficient of determination; the most parsimonious regression model was identified with the Akaike

203 information criterion corrected for small sample sizes (AICc); and we used model averaging to
204 estimate parameter and associated unconditional standard errors based on the subset of top ranking
205 models for which the sum of AICc weights reached ≥ 0.95 (Burnham & Anderson 2002). To determine
206 whether the inclusion of tree characteristics improved the models' predictive power, we used
207 General Linear Mixed Models (GLMMs). Total and *Lobarion* epiphytic macrolichens richness and
208 cover at each tree ($n = 420$) were used as dependent variables, as well as the standardized richness.
209 We then investigated whether diversity patterns were predicted by tree species and diameter
210 variables, as well as the most influential environmental variables at the plot scale (i.e. temperature
211 and mean canopy openness), using 12 a priori candidate linear models, plus the null model
212 (Appendix S3). For *Lobarion* species, observed on deciduous trees only (European beech, $n = 28$;
213 other deciduous trees, $n = 7$), we tested all possible combinations of models formed by tree diameter
214 and the most influential environmental variables at the plot scale (n models = 5). We then fit Poisson
215 linear mixed models for richness and negative binomial linear mixed models for cover with "plot" as
216 a random effect and "latitude" as a covariate in all the candidate models. We used the marginal
217 coefficient of determination for fixed effect parameters alone to estimate the variance explained by
218 the GLMMs (Nakagawa et al. 2017). We then ranked the models according to their AICc values and
219 used model averaging to estimate the parameters.

220 To determine whether epiphytic macrolichen composition was influenced by forest continuity, stand
221 maturity or their interaction, we performed PERMANOVA (i.e. between-groups) and PERMDISP (i.e.
222 within-group) analyses (Anderson & Walsh 2013) based on a Bray-Curtis distance, with 999
223 permutations. We then used canonical analysis of principal coordinates (CAP, Anderson & Willis
224 2003) based on a Bray-Curtis distance matrix, with 999 permutations, at the plot scale, to determine
225 whether climate, stand or landscape variables explain epiphytic macrolichen assemblage variations;
226 at the tree scale, to determine whether the inclusion of tree characteristics allows for a better
227 understanding of epiphytic macrolichens assemblage variations (after removing trees for which no
228 macrolichen species were recorded ($n = 103$)). At the plot and tree scales, we calculated the marginal

229 contribution of all independent variables to total constrained inertia and tested for their individual
230 significance (after all other variables were partialled out). Finally, composition analyses of *Lobarion*
231 species were not performed because they were rarely observed at the plot ($n = 23$) and tree ($n = 35$)
232 scales.

233

234 **RESULTS**

235 **Variations in environmental variables in relation to forest continuity and stand maturity**

236 Stand and landscape variables varied according to forest continuity and stand maturity classification
237 (Table 1). Indeed, mean canopy openness, stem basal area and the number of very large trees
238 increased from mature to overmature stands. Compared to recent forest sites, ancient forest sites
239 were included in a less diversified matrix, that contained more forests overall, and were located at a
240 greater distance from the forest edge. Climate variables, on the other hand, were not clearly related
241 to forest continuity or to stand maturity. Only total annual precipitation increased from ancient to
242 recent forest sites, even though the effect size was low.

243 The interaction term between forest continuity and stand maturity was non-significant for almost all
244 the tested variables (Table 1), indicating that variations were consistent between ancient and recent
245 forests, at a comparable level of maturity.

246 **Diversity patterns for epiphytic macrolichens at the stand and tree scales**

247 Overall, 33 species of epiphytic macrolichens were recorded at the 70 sites (Appendix S4), including
248 10 *Lobarion* species. Total and *Lobarion* species richness ranged from 1-16 species and from 0-4
249 species, and averaged six species ($SD \pm 3.55$) and 0.5 species ($SD \pm 0.91$) per site, respectively.

250 At the stand scale, two-way ANOVAs revealed no difference in total or *Lobarion* richness or cover
251 between ancient and recent forests, mature and overmature stands or between ancient-mature,
252 ancient-overmature, recent-mature and recent-overmature stands (Appendix S5). GLMs results
253 showed that total richness and cover, as well as standardized total richness, were best predicted by
254 the same model, which accounted for temperature and mean canopy openness (Table 2). For

255 Lobarion species, GLMs results showed that richness was best predicted by a model accounting for
256 basal area and forest proportion in the surrounding landscape, that cover was best predicted by the
257 null model and that standardized richness was best predicted by a model accounting for cover only.
258 Except for total richness (AICc weights = 0.984), model selection uncertainty still remained for all the
259 dependent variables. Model averaging revealed that total richness and cover, as well as standardized
260 richness, increased with decreasing temperatures and with increasing mean canopy openness (Table
261 3). For Lobarion species, richness increased with stand basal area. However, for both Lobarion
262 richness and cover, the null model was among the top-ranking models.

263 At the tree scale, GLMMs results showed that total richness and cover were best predicted by the
264 same model, which accounted for temperature, mean canopy openness and tree species, while
265 standardized total richness was best predicted by a model accounting for lichen cover, temperature
266 and tree species (Table 4). For Lobarion species, GLMMs results showed that richness and cover were
267 both best predicted by the same model, which accounted for mean canopy openness and tree
268 diameter, while standardized Lobarion richness was best predicted by a model accounting for lichen
269 cover, mean canopy openness and tree diameter (Table 4). However, model selection uncertainty
270 still remained for all the dependent variables. Model averaging revealed that total richness and cover
271 increased with mean canopy openness but that total richness and cover, as well as standardized total
272 richness, decreased with increasing temperature (Table 5). Moreover, with Silver fir as a reference,
273 total richness and cover, as well as standardized richness, decreased on European beech and other
274 deciduous trees, while cover only decreased on Norway spruce. For Lobarion species, richness and
275 cover, as well as standardized richness, increased with tree diameter, while standardized richness
276 only increased with mean canopy openness (Table 5).

277 **Variations in epiphytic macrolichen composition at stand and tree scales**

278 Lichens composition was influenced neither by forest continuity (PERMANOVA pseudo- $F_{1,68} = 0.661$,
279 $p = 0.706$), nor by stand maturity (PERMANOVA pseudo- $F_{1,68} = 1.712$, $p = 0.116$) or maturity-
280 continuity interaction (PERMANOVA pseudo- $F_{1,68} = 0.606$, $p = 0.762$). Moreover, PERMDISP revealed

281 no significant differences in the average within-group distances, thus supporting the absence of
282 variation in assemblage structure among treatments.

283 At the stand scale, CAP ordination revealed that 22.5% ($p = 0.001$) of the variation in species
284 composition was explained by environmental variables (Figure 2 & Appendix S6 for elementary
285 contributions of variables to inertia). The first CAP axis was positively related to latitude (12.9%, $p =$
286 0.001) and temperature (17.6%, $p = 0.001$) but negatively related to canopy openness (15.2%, $p =$
287 0.005). The second CAP axis was positively related to precipitation (14.4%, $p = 0.043$). All the other
288 variables did not significantly influence species composition. At the tree scale, CAP ordination
289 revealed that 15.1% ($p = 0.001$) of the variation in species composition was explained by tree
290 characteristics and environmental variables (Figure 2 & Appendix S7). The first CAP axis was
291 positively related to latitude (8.3%, $p = 0.001$) and temperature (14.1%, $p = 0.001$). The second CAP
292 axis was positively related to canopy openness (14.5%, $p = 0.001$) and negatively related to tree
293 diameter (3.6%, $p = 0.001$). Also, tree species explained a large part of the variation in species
294 composition (31.1%, $p = 0.001$), with a clear pattern opposing deciduous from coniferous trees along
295 the two CAP axes.

296

297 **DISCUSSION**

298 In unfragmented mountain forests, our results clearly show that climate parameters, light availability
299 at the stand scale and host-tree characteristics were the major drivers of epiphytic macrolichen
300 diversity and composition. Neither forest habitat qualities, i.e. maturity and continuity factors, nor
301 stand- and landscape-associated variables, affected by present and past human activities, were of
302 any inferential value.

303 **Forest continuity and stand maturity are not the main drivers of epiphytic macrolichen** 304 **assemblages**

305 Contrary to our expectations, the assemblage patterns of epiphytic macrolichens were not influenced
306 by forest continuity and landscape-associated variables. This surprising lack of a legacy effect is

307 interesting given the large number of studies that have demonstrated the influence of forest
308 continuity on biodiversity (Hermy & Verheyen 2007). Previous studies have, indeed, reported a
309 significant effect of forest continuity on lichens (Fritz, Gustafsson, et al. 2008; Moning et al. 2009;
310 Marmor et al. 2011), especially on the most demanding species, such as the *Lobarion* macrolichens
311 and the cyanolichens (Rose 1976; Kuusinen 1996; Ellis & Coppins 2007). Nonetheless, studies
312 conducted in forest-dominated landscapes with good habitat connectivity, as was the case in the
313 Northern Alps, only found a limited effect of forest continuity and landscape factors on lichen
314 assemblages (Dittrich et al. 2013; Király et al. 2013; Ódor et al. 2013). . Fragmentation worsens
315 dispersal limitations (Jamoneau et al. 2012), and since colonization efficiency depends on habitat
316 availability at the landscape scale (De Frenne et al. 2011), the lichen species in our study area appear
317 to have been able to rapidly colonize recent forests. Moreover, as elsewhere in European mountain
318 areas (e.g. Gellrich et al. 2007), reforestation has largely occurred next to ancient forests, thus
319 reducing the distance to habitat source and limiting dispersal barriers within the habitat matrix
320 (Honnay et al. 2002). For all these reasons, we infer that the distance between regeneration units
321 and potential sources of propagules in the Northern Alps is sufficiently low to not limit epiphytic
322 macrolichen dispersal and establishment in recent forests (e.g. Hilmo 2002; Werth et al. 2006).
323 However, even in this unfragmented forest landscape, forest continuity and landscape variables
324 cannot be ruled out as influencing factors, particularly for dispersal-limited epiphytic species with
325 strong substrate-specific requirements such as certain crustose and leprose lichen species (e.g.
326 Marmor et al. 2011; Kubiak & Osyczka 2017).

327 In addition, assemblage patterns were not influenced by stand maturity and stand-associated
328 variables. These results contrast with current knowledge on the importance of old-growth forest
329 attributes for biodiversity. Indeed, numerous studies have pointed out a direct link between the
330 availability of larger, older trees at the stand scale and lichen diversity (Kuusinen 1996; Fritz,
331 Niklasson, et al. 2008; Ranius et al. 2008; Marmor et al. 2011). In our study area, the availability of
332 large standing trees did not structure diversity and composition, even though we inventoried five

333 times as many such trees in overmature than mature stands. This lack of any stand-maturity
334 influence on epiphytic macrolichens may be due to the relatively high habitat quality of both the
335 mature and overmature stands in the Alps resulting from selective-cutting management practices
336 (Nascimbene et al. 2007; Dymytrova et al. 2014). Combined with landscape homogeneity, this may
337 have facilitated species dispersion and establishment on a large number of host trees (Ellis 2012;
338 Nascimbene, Thor, et al. 2013). Moreover, as in the Italian Alps (Nascimbene, Dainese, et al. 2013),
339 we found that light conditions was one of the most powerful predictor of total epiphytic macrolichen
340 diversity and composition at the stand scale. Indeed, it is well known that lichen species avoid shady
341 conditions and that these photosynthetic organisms benefit from an increase in canopy openness
342 (Uliczka & Angelstam 1999; Moning et al. 2009; Jüriado et al. 2009; Ódor et al. 2013). Overall, since
343 availability and heterogeneity of light are expected to increase during forest succession in adult
344 stands due to changes in the canopy - gap structure, our results confirm the positive effect of
345 management practices aiming at maintaining or enhancing stand structural heterogeneity (Ellis 2012;
346 Nascimbene, Thor, et al. 2013), such as selective cutting and retention forestry (Gustafsson et al.
347 2012).

348 **Climate and tree species characteristics better explain epiphytic macrolichen assemblages**

349 Among all of the environmental variables we tested, temperature best explained epiphytic
350 macrolichen assemblages at the stand scale, with higher temperatures producing an overall negative
351 effect on diversity. This result is quite surprising given that, in our sampling design, we controlled for
352 differences in altitude among treatments. The effect of temperature was thus more likely due to
353 small intra-group variations (i.e. standard deviation in altitude = ± 140 m) than to broad altitudinal
354 gradients. Indeed, in mountain areas, altitude and exposure exacerbate climatic differences, and
355 substantial changes can be found over small distances. Climate is known to greatly influence lichen
356 species distribution at large scale (Werth et al. 2005; Ellis & Coppins 2007). At a smaller scale,
357 however, it has been suggested that stand structure parameters would better explain lichen diversity
358 patterns than would climatic parameters (Moning et al. 2009). Controlling for differences in forest

359 structure, Bässler et al. (2016) recently showed that lichen diversity increased with decreasing
360 temperatures in Bohemian mountain forests, and that this increase was above all driven by an
361 increase in the number of foliose and fruticose species. These findings corroborate previous ones in
362 the Alps (Nascimbene & Marini 2015) and Carpathian Mountains (Dymytrova et al. 2014), and give
363 weight to the view that macrolichen diversity peaks at mid elevations (Rapai et al. 2012). We believe
364 that the strong effect of temperature we found in the Northern Alps is related to optimal
365 performances of the mountain beech-fir macrolichen community in colder climates. This view is
366 supported by the fact that we recorded numerous species (e.g. *Hypogymnia physodes*, *Parmelia*
367 *saxatilis*, *Parmeliopsis ambigua*) characteristic of a cold-humid climate niche (Giordani & Incerti
368 2008). However, contrary to numerous other studies (e.g. Giordani & Incerti 2008; Marini et al. 2011;
369 Coyle & Hurlbert 2016), we found no strong relationship between atmospheric water supply and
370 epiphytic macrolichen assemblages. This may be due to the substantial yearly amounts of rainfall
371 occurring in the three studied mountain ranges (mean annual precipitation >1500 mm).

372 Tree characteristics greatly influenced assemblages of epiphytic macrolichens. Especially, total
373 species richness and cover were higher on silver fir than on other tree species, while *Lobarion* species
374 were exclusively found on deciduous trees. Tree species identity is a well-known driver of epiphytic
375 lichen composition and numerous studies have also reported a significant effect on species diversity
376 (Moning et al. 2009; Király et al. 2013; Ódor et al. 2013). Specifically, in mountain beech-fir forests, it
377 has been shown that the two dominant tree species hosted different communities, thus increasing
378 lichen richness at the stand scale (Nascimbene et al. 2009). Host-use preferences is closely related to
379 differences in the physical and chemical properties of the bark substratum (Ellis 2012; Nascimbene,
380 Thor, et al. 2013). Our findings support the common suggestion that conservation-oriented forest
381 management should maintain tree species diversity (Ellis 2012; Nascimbene, Thor, et al. 2013; Ódor
382 et al. 2013). However, in our study, the greater species richness we found on silver fir was more
383 probably linked to a sampling bias, since the sampled fir trees had a larger diameter than the other
384 sampled species (Silver fir, DBH = 68 cm ± 15; Norway spruce, DBH = 58 cm ± 11; European beech,

385 DBH = 43 cm \pm 15; other deciduous trees, DBH = 41 cm \pm 10). Indeed, high epiphytic lichen diversity is
386 often reported on larger trees (Moning et al. 2009; Jüriado et al. 2009), in line with our results on
387 *Lobarion* diversity and composition. Epiphytic macrolichen conservation, particularly for *Lobarion*
388 species, would benefit from the maintenance of very large trees, especially deciduous trees.

389 **Conclusion**

390 The effects of forest continuity and stand maturity on lichen assemblages are supposedly context-
391 dependent. Within our relatively homogeneous mountain forests, neither epiphytic macrolichen
392 diversity nor composition responded to stand maturity and forest continuity. Using lichen species as
393 indicators of ancient forests must therefore be cautious (Nordén & Appelqvist 2001; Fenton &
394 Bergeron 2008). Our results point out the importance of structural heterogeneity at the stand and
395 tree scales in improving both light and tree-diameter diversity. In mixed mountain forests, selection
396 cutting which maintains an uneven-aged structure with trees of all sizes and species should therefore
397 be promoted. These management practices make it possible to balance wood production and
398 biodiversity conservation, even for the demanding *Lobarion* macrolichens. Finally, we found an
399 important negative effect of rising temperatures on assemblage patterns suggesting that global
400 warming is probably the most significant threat for macrolichen conservation in temperate mountain
401 forests (e.g. Nascimbene et al. 2016). Overall then, assemblage patterns are not regulated by single-
402 scale environmental parameters but by processes acting at both regional and local scales (Coyle &
403 Hurlbert 2016). Conservation strategies should therefore be systematically based on a multiple-scale
404 environmental evaluation.

405

406 **DATA ACCESSIBILITY STATEMENT**

407 The research data supporting this publication are provided in Supplementary Material (Online
408 Publication Only).

409

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413

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587

588 **SUPPORTING INFORMATION**

589 **Appendix S1.** Correlation matrix of environmental variables used to model macrolichen assemblages.

590 **Appendix S2.** Candidate models used to model macrolichen diversity at the stand scale.

591 **Appendix S3.** Candidate models used model macrolichen diversity at the tree scale.

592 **Appendix S4.** List of epiphytic macrolichen species recorded in the Northern Alps.

593 **Appendix S5.** Variations in macrolichen diversity in relation to forest continuity and stand maturity
594 factors.

595 **Appendix S6.** Elementary contributions of environmental variables to inertia in the CAP of
596 macrolichens communities.

597 **Appendix S7.** Elementary contributions of tree characteristics and environmental variables to inertia
598 in the CAP of macrolichens communities.

599 **Appendix S8.** Raw data at the stand scale.

600 **Appendix S9.** Raw data at the tree scale.

601 **Appendix S10.** Site by species matrix of epiphytic macrolichens at the stand scale.

602 **Appendix S11.** Site by species matrix of epiphytic macrolichens at the tree scale.

603

604 Table 1. Variations in site, climate, stand and landscape variables between ancient-mature sites (Anc-Mat), ancient-overmature sites (Anc-Ove), recent-
605 mature sites (Rec-Mat) and recent-overmature sites (Rec_Ove) in the French Northern Alps (DBH = diameter at breast height). Two-way ANOVAs test the
606 significance of environmental variables to forest continuity (FC), stand maturity (SM) and their interaction (INTER).

Variables	Description	Anc-Mat	Anc-Ove	Rec-Mat	Rec-Ove	FC	SM	INTER
		Mean (\pm SD)	Mean (\pm SD)	Mean (\pm SD)	Mean (\pm SD)	p-value	p-value	p-value
Site variables								
Lati	Latitude (decimal degrees)	45.33 (\pm 0.23)	45.50 (\pm 0.23)	45.44 (\pm 0.23)	45.50 (\pm 0.22)	0.164	0.035	0.340
Long	Longitude (decimal degrees)	5.78 (\pm 0.26)	5.94 (\pm 0.25)	5.91 (\pm 0.25)	5.94 (\pm 0.27)	0.135	0.081	0.304
Alti	Altitude (meters)	1179 (\pm 129)	1145 (\pm 145)	1073 (\pm 133)	1102 (\pm 144)	0.024	0.457	0.348
Slope	Slope (%)	23.56 (\pm 6.56)	24.98 (\pm 8.38)	25.63 (\pm 8.14)	25.61 (\pm 7.08)	0.410	0.571	0.691
Expo	Exposure (degrees)	231.8 (\pm 96.8)	232.7 (\pm 115.2)	217.6 (\pm 114.8)	246.3 (\pm 112.3)	0.698	0.981	0.599
Climate variables								
Temp	Mean annual temperature ($^{\circ}$ C)	6.73 (\pm 0.58)	6.90 (\pm 0.78)	7.14 (\pm 0.60)	7.05 (\pm 0.70)	0.069	0.444	0.426
Precip	Sum annual precipitation (mm)	1579 (\pm 272)	1687 (\pm 151)	1746 (\pm 198)	1628 (\pm 218)	0.027	0.150	0.038
Humi	Mean relative humidity (g/kg)	5.67 (\pm 0.30)	5.70 (\pm 0.24)	5.60 (\pm 0.22)	5.74 (\pm 0.31)	0.486	0.745	0.440
Stand variables								

Canop	Mean canopy openness (%)	8.39 (± 3.44)	13.52 (± 6.01)	9.02 (± 4.41)	11.31 (± 6.14)	0.743	0.006	0.267
Basal_area	Total stems basal area (m ²)	5.65 (± 1.59)	6.68 (± 1.89)	6.26 (± 1.93)	7.96 (± 1.73)	0.270	0.045	0.489
Large_trees	Number of very large trees (DBH > 62.5 cm)	0.77 (± 1.07)	5.93 (± 3.83)	0.73 (± 0.59)	5.83 (± 2.77)	0.693	0.000	0.971
Landscape variables (500-m-radius)								
Alpha_LU	Land-use diversity	2.59 (± 1.14)	2.40 (± 0.91)	3.33 (± 0.90)	2.78 (± 1.00)	0.000	0.429	0.528
Dist_Forest	Distance to the nearest forest edge (meters)	557 (± 489)	554 (± 373)	230 (± 131)	468 (± 313)	0.002	0.588	0.107
Prop_Forest	Forest proportion (%)	90.79 (± 11.74)	94.56 (± 9.22)	79.72 (± 14.79)	93.06 (± 8.20)	0.006	0.364	0.119

607

608 Table 2. Top-ranking models among 49 a priori models predicting diversity patterns of total and
 609 *Lobarion* epiphytic macrolichens at the stand scale in the French Northern Alps, as assessed with
 610 Akaike's information criterion corrected for small sample size (AICc). Number of estimated
 611 parameters including the intercept (k), AICc, , AICc weight (W), adjusted coefficient of determination
 612 (R^2_{adj}) and evidence ratio (ER), i.e. Akaike weight of the best model/Akaike weight of the second best
 613 model, are provided.

Dependent variable	Model	k	AICc	W	R^2_{adj}	ER
Total richness	Canop + Temp	4	332.8	0.984	0.591	328.00
Total cover	Canop + Temp	5	663.3	0.427	0.421	2.98
Standardized total richness	Cover + Canop + Temp	5	304.8	0.356	0.736	2.25
Lobarion richness	Basal_area + Prop_Forest	4	140.0	0.127	0.151	1.03
Lobarion cover	Null	2	213.6	0.161	0.000	2.77
Standardized Lobarion richness	Cover	2	84.9	0.261	0.667	5.22

614

615 Table 3. Relative importance (Imp.), average coefficients (Estimate (\pm SE)) and confidence intervals (95% CI) for each variable predicting total and *Lobarion*
 616 epiphytic macrolichen richness and cover at the stand scale in the French Northern Alps. The 95% confidence interval of coefficients shaded excluded 0.

Parameter	Total richness			Total cover			Standardized total richness		
	Imp.	Estimate (\pm SE)	(95% CI)	Imp.	Estimate (\pm SE)	(95% CI)	Imp.	Estimate (\pm SE)	(95% CI)
Cover	NA	NA	NA	NA	NA	NA	1.00	0.005 (\pm 0.001)	(0.003; 0.007)
Lati	1	-0.737 (\pm 0.222)	(-1.172; -0.302)	1.00	-1.424 (\pm 0.455)	(-2.315; -0.533)	1.00	-0.183 (\pm 0.252)	(-0.677; 0.311)
Temp	1	-0.343 (\pm 0.083)	(-0.506; -0.180)	0.92	-0.489 (\pm 0.149)	(-0.781; -0.198)	0.99	-0.273 (\pm 0.087)	(-0.444; -0.103)
Precip	NA	NA	NA	0.28	-0.001 (\pm 0.001)	(-0.002; 0.000)	0.07	0.000 (\pm 0.000)	(-0.001; 0.001)
Humi	NA	NA	NA	0.17	-3.405 (\pm 2.583)	(-8.467; 1.658)	0.08	0.765 (\pm 1.198)	(-1.583; 3.113)
Canop	1	0.353 (\pm 0.091)	(0.175; 0.531)	0.52	0.447 (\pm 0.174)	(0.106; 0.788)	0.38	0.193 (\pm 0.098)	(0.000; 0.386)
Basal_area	NA	NA	NA	0.06	-0.323 (\pm 0.337)	(-0.984; 0.338)	0.06	0.116 (\pm 0.180)	(-0.237; 0.469)
Large_Tree	NA	NA	NA	0.08	-0.163 (\pm 0.117)	(-0.394; 0.067)	0.05	0.005 (\pm 0.061)	(-0.114; 0.124)
Alpha_LU	NA	NA	NA	0.02	-0.047 (\pm 0.091)	(-0.225; 0.131)	0.06	-0.027 (\pm 0.053)	(-0.132; 0.078)
Dist_Forest	NA	NA	NA	0.02	-0.030 (\pm 0.120)	(-0.266; 0.206)	0.06	0.032 (\pm 0.069)	(-0.103; 0.166)
Prop_Forest	NA	NA	NA	0.02	0.031 (\pm 0.079)	(-0.123; 0.185)	0.09	0.047 (\pm 0.046)	(-0.044; 0.137)

617

Parameter	<i>Lobarion</i> richness			<i>Lobarion</i> cover			Standardized <i>Lobarion</i> richness		
	Imp.	Estimate (\pm SE)	(95% CI)	Imp.	Estimate (\pm SE)	(95% CI)	Imp.	Estimate (\pm SE)	(95% CI)
Cover	NA	NA	NA	NA	NA	NA	1.00	0.332 (\pm 0.046)	(0.243; 0.421)
Lati	0.97	-0.556 (\pm 0.783)	(-2.091; 0.979)	0.83	0.243 (\pm 1.409)	(-2.518; 3.004)	0.73	0.080 (\pm 0.720)	(-1.331; 1.491)
Temp	0.06	0.127 (\pm 0.276)	(-0.414; 0.668)	0.11	0.238 (\pm 0.508)	(-0.758; 1.234)	0.12	-0.143 (\pm 0.314)	(-0.758; 0.472)
Precip	0.14	-0.001 (\pm 0.001)	(-0.003; 0.001)	0.20	-0.002 (\pm 0.002)	(-0.006; 0.001)	0.09	0.000 (\pm 0.001)	(-0.002; 0.003)
Humi	0.06	-1.915 (\pm 4.603)	(-10.937; 7.108)	0.12	-6.583 (\pm 8.437)	(-23.120; 9.953)	0.13	2.593 (\pm 4.353)	(-5.939; 11.125)
Canop	0.25	0.481 (\pm 0.315)	(-0.136; 1.099)	0.28	0.900 (\pm 0.531)	(-0.141; 1.942)	0.12	0.118 (\pm 0.368)	(-0.604; 0.839)
Basal_area	0.79	1.576 (\pm 0.622)	(0.357; 2.795)	0.18	0.957 (\pm 1.073)	(-1.146; 3.059)	0.11	-0.113 (\pm 0.556)	(-1.202; 0.977)
Large_Tree	0.20	0.282 (\pm 0.258)	(-0.225; 0.788)	0.10	0.196 (\pm 0.370)	(-0.529; 0.922)	0.09	0.003 (\pm 0.217)	(-0.423; 0.429)
Alpha_LU	0.05	-0.029 (\pm 0.186)	(-0.393; 0.335)	0.09	0.084 (\pm 0.328)	(-0.558; 0.727)	0.17	-0.150 (\pm 0.206)	(-0.554; 0.253)
Dist_Forest	0.12	0.270 (\pm 0.227)	(-0.174; 0.714)	0.17	0.466 (\pm 0.447)	(-0.410; 1.341)	0.16	-0.538 (\pm 0.683)	(-1.877; 0.800)
Prop_Forest	0.16	0.229 (\pm 0.165)	(-0.094; 0.552)	0.15	0.247 (\pm 0.321)	(-0.383; 0.876)	0.18	0.373 (\pm 0.517)	(-0.639; 1.386)

618 Table 4. Top-ranking models among 13 a priori models predicting diversity patterns for total
619 epiphytic macrolichens, and among 5 a priori models predicting diversity patterns for *Lobarion*
620 epiphytic macrolichens, at the tree scale in the French Northern Alps, as assessed with Akaike's
621 information criterion corrected for small sample size (AICc). Number of estimated parameters
622 including the intercept (k), AIC_c, AICc weight (W), marginal coefficient of determination for fixed
623 effect (R^2_{GLMM}) and evidence ratio (ER), i.e. Akaike weight of the best model/Akaike weight of the
624 second best model, are provided.

Dependent variable	Model	k	AICc	W	R^2_{GLMM}	ER
Total richness	Temp + Canop + Species	8	1427.6	0.538	0.362	1.55
Total cover	Temp + Canop + Species	9	2384.5	0.451	0.326	1.19
Standardized total richness	Cover + Temp + Species	8	1319.7	0.468	0.428	1.75
<i>Lobarion</i> richness	Canop + Diam	5	223.0	0.477	0.093	1.95
<i>Lobarion</i> cover	Canop + Diam	6	318.8	0.477	0.100	1.88
Standardized <i>Lobarion</i> richness	Cover + Canop + Diam	6	145.6	0.550	0.319	2.91

625

626 Table 5. Relative importance (Imp.), average coefficients (Estimate (\pm SE)) and confidence intervals (95% CI) for each variable predicting total and *Lobarion*
 627 epiphytic macrolichen richness and cover at the tree scale in the French Northern Alps. The 95% confidence interval of coefficients shaded excluded 0.

Parameter	Total richness			Total cover			Standardized richness			
	Imp.	Estimate (\pm SE)	(95% CI)	Imp.	Estimate (\pm SE)	(95% CI)	Imp.	Estimate (\pm SE)	(95% CI)	
Cover	NA	NA	NA	NA	NA	NA	1.00	0.397 (\pm 0.031)	(0.335; 0.459)	
Lati	1.00	-0.249 (\pm 0.073)	(-0.393; -0.105)	1.00	-0.388 (\pm 0.110)	(-0.603; -0.173)	1.00	-0.079 (\pm 0.048)	(-0.173; 0.014)	
Temp	1.00	-0.299 (\pm 0.077)	(-0.449; -0.149)	1.00	-0.347 (\pm 0.111)	(-0.565; -0.129)	1.00	-0.204 (\pm 0.050)	(-0.301; -0.107)	
Canop	0.89	0.180 (\pm 0.070)	(0.042; 0.317)	0.85	0.252 (\pm 0.105)	(0.046; 0.459)	0.36	0.044 (\pm 0.046)	(-0.045; 0.133)	
Tree_diam	0.40	0.067 (\pm 0.059)	(-0.048; 0.182)	0.47	0.107 (\pm 0.079)	(-0.048; 0.263)	0.26	0.010 (\pm 0.051)	(-0.089; 0.110)	
Tree_sp	Fir - Spruce	1.00	-0.166 (\pm 0.101)	(-0.364; 0.032)	1.00	-0.347 (\pm 0.172)	(-0.684; -0.010)	1.00	0.084 (\pm 0.097)	(-0.106; 0.274)
	Fir - Beech	1.00	-0.865 (\pm 0.101)	(-1.063; -0.668)	1.00	-1.281 (\pm 0.144)	(-1.563; -0.998)	1.00	-0.427 (\pm 0.093)	(-0.608; -0.245)
	Fir - Decid.	1.00	-0.520 (\pm 0.184)	(-0.881; -0.160)	1.00	-0.680 (\pm 0.258)	(-1.185; -0.175)	1.00	-0.245 (\pm 0.174)	(-0.585; 0.096)

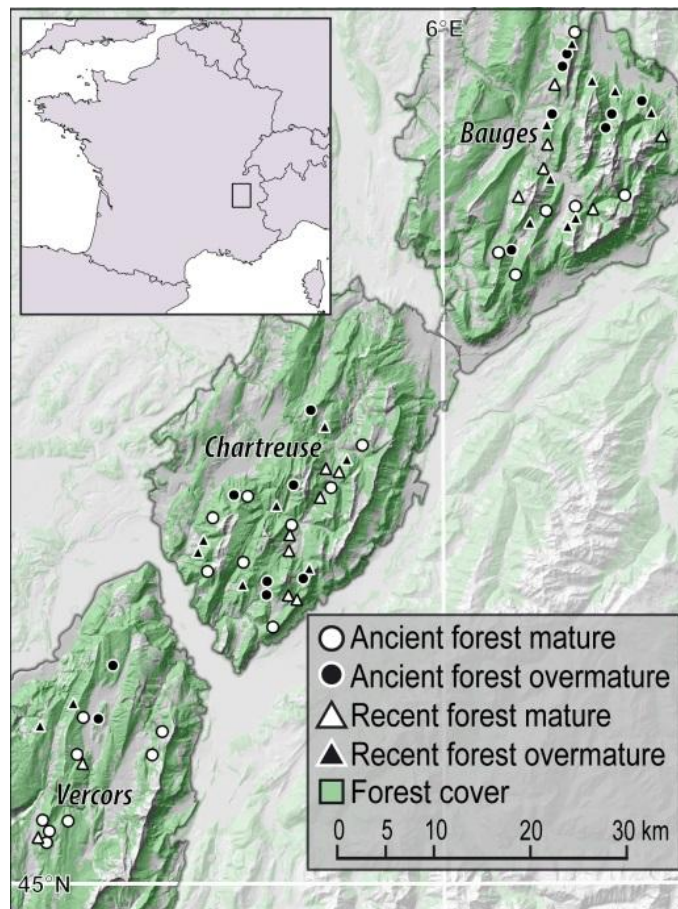
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Parameter	<i>Lobarion</i> richness			<i>Lobarion</i> cover			Standardized <i>Lobarion</i> richness		
	Imp.	Estimate (\pm SE)	(95% CI)	Imp.	Estimate (\pm SE)	(95% CI)	Imp.	Estimate (\pm SE)	(95% CI)
Cover	NA	NA	NA	NA	NA	NA	1.00	0.575 (\pm 0.059)	(0.460; 0.691)
Lati	1.00	0.037 (\pm 0.239)	(-0.432; 0.506)	1.00	0.163 (\pm 0.345)	(-0.513; 0.839)	1.00	0.548 (\pm 0.171)	(0.212; 0.883)
Temp	0.26	0.057 (\pm 0.263)	(-0.458; 0.573)	0.26	0.081 (\pm 0.379)	(-0.661; 0.823)	0.27	-0.022 (\pm 0.179)	(-0.372; 0.329)
Canop	0.66	0.446 (\pm 0.243)	(-0.030; 0.922)	0.66	0.640 (\pm 0.353)	(-0.051; 1.331)	0.74	0.328 (\pm 0.159)	(0.017; 0.640)
Tree_diam	1.00	0.486 (\pm 0.161)	(0.171; 0.800)	1.00	0.693 (\pm 0.236)	(0.230; 1.156)	1.00	0.291 (\pm 0.109)	(0.078; 0.504)
Tree_sp	Fir - Spruce	NA	NA	NA	NA	NA	NA	NA	NA
	Fir - Beech	NA	NA	NA	NA	NA	NA	NA	NA
	Fir - Decid.	NA	NA	NA	NA	NA	NA	NA	NA

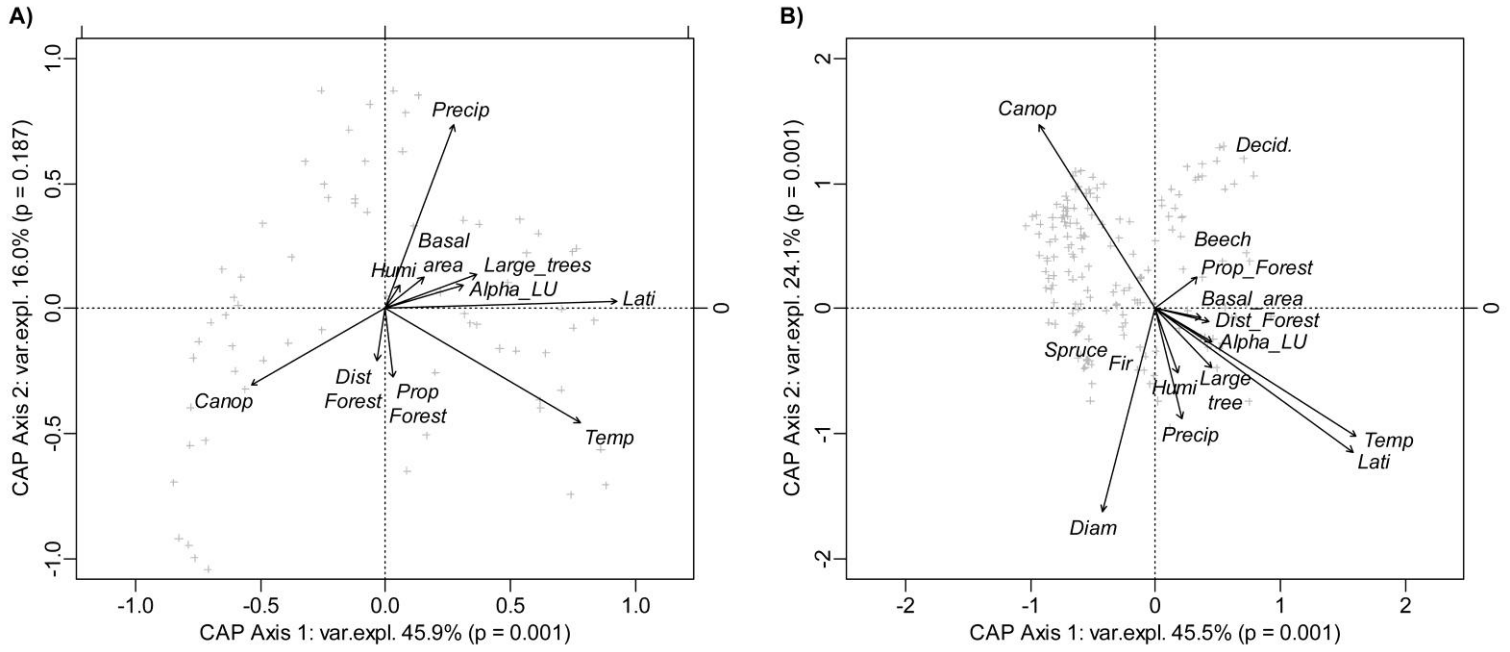
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630 Figure. 1. Study area and distribution of sampling sites among ancient and recent forests and mature
631 and overmature stands in the French Northern Alps, France.

632



633 Figure 2. Canonical analysis of principal coordinates (CAP) constrained ordination of epiphytic
 634 macrolichens communities in relation to A) climate, stand and landscape variables at the stand scale
 635 (n = 70) and B) tree characteristics and environmental variables at the tree scale (n = 317).



636